Do trees suppress grass fuel loads? Canopy cover effects in South African savannas

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ABSTRACT

Continental scale analysis of the savanna biome indicated that fire did not spread at tree canopy cover above 40%. This study investigates this relationship in a field study. It is possible that the type of tree (forest vs. savanna) may influence the amount of shade experienced by the understory and therefore this study also explores differences in LAI between congeneric pairs of forest and savanna tree species. Data were collected in two major South African savanna parks. Plots were set out to measure grass biomass in reference to canopy cover in both Kruger National Park (n=60) and the Hluhluwe-iMfolozi Game Reserve (n=82). Seven congeneric pairs were selected to compare leaf area and LAI between forest and savanna tree species using a destructive method. Against expectations, it was only when canopy cover reached 80% that grass fuel load was too low to support fire spread in all Kruger National Park plots (Pr=0) and 89% of the Hluhluwe-iMfolozi Game Reserve plots (Pr=0.11). No consistent, general relationships were evident with leaf area or LAI in comparisons between forest-savanna congeneric pairs. The significance of these findings and future direction is discussed.

Key words: canopy cover, grass biomass, fire, leaf area, LAI

which is?

No real description of this as an indirect method – probability of fire not discussed

INTRODUCTION

The savanna biome is a dynamic region defined by the presence of extensive grass layers interspersed with trees (Sankaran *et al.* 2005, 2008). Savannas are diverse ecosystems and support some of the last mega-herbivores of this age. In addition these ecosystems are of significant importance to the human population, covering expansive areas of earth's terrestrial surface and supporting major livestock biomass (Scholes & Archer 1997). Over 50% of the African continent is covered by savanna vegetation and these mixed tree and grass communities are important in the relevant economies both as tourist attractions and for agriculture. As a result much of the savanna biome within Africa and indeed the world is under extensive management. To ensure that these systems and their related industries are protected it is necessary to develop an understanding of their dynamics. This paper focuses on Southern African savanna systems and looks into the impacts of trees on grass cover in two major savanna parks, Kruger National Park (KNP) and the Hluhluwe-iMfolozi Game Reserve (HIP).

Sankaran *et al.* (2005, 2008) found that woody cover is largely limited by mean annual precipitation until a threshold of 650mm, above which disturbances and other regulatory variables are the main limitation to woody cover. It is clear that while low rainfall limits maximum woody cover, rainfall alone fails to explain what limits woody plants in wetter regions that should support closed canopy forest. This issue is highlighted in regions where open grasslands occur in the presence of dense forests, creating abrupt boundaries (Warman and Moles 2009). The relationships between woody cover and grasses within savanna systems are complex and result from a range of regulatory environmental variables (Roques *et al.* 2001; Bond and Archibald 2003; Bond *et al.* 2003; Meyer *et al.* 2007a; Sankaran *et al.* 2005, 2008). These regulatory variables fall within two broad categories: "top-down" and "bottom-up" controls (Staver *et al.* 2009; Weltzin and Coughenour 1990). Bottom-up

controls encompass resource-limiting factors such as water availability, soil nutrients, and access to light (Weltzin and Coughenour 1990), while top-down controls describe disturbance regimes such as fire and herbivory (Bond 2008). It has recently been shown that at the continental scale both bottom up and top down controls act to limit woody cover in savanna ecosystems. In particular, continental scale data indicate that fire is influential in limiting maximum tree cover within high rainfall African systems (Bond *et al.* 2003; 2008; Lehmann *et al.* 2011; Staver *et al.* 2011). Fire limits woody cover by preventing tree recruitment, as saplings are continually stuck in what has been termed the "fire-trap" until they are afforded the opportunity to escape by growing into adult trees (Bond and Midgley 2001). The asynchronous succession to wooded states in the absence of fire and restriction of woody plant growth from attaining maximum potential cover in the presence of fire maintains the coexistence of trees and grasses (Meyer *et al.* 2007a; Staver *et al.* 2009). As fire is such a defining factor within savanna systems the focal area of this study is the impact of trees on the fuel load available to fires and specifically the threshold below which fire fails to spread through woodland due to limited fuel availability.

The density of trees is not consistent for a given savanna site and varies depending on fire return times. The effects of extending fire return intervals have been demonstrated in numerous fire exclusion experiments (Silva *et al.* 1991; Bond and Archibald 2003; Higgins *et al.* 2007). These indicate that sapling transitions to large tree size will increase if the interval between fires is long, causing the system to shift towards a wooded state (Silva *et al.* 1991; Beckage and Stout 2000; Bond and Archibald 2003; Beckage *et al.* 2006; Higgins *et al.* 2007). It is thought that an increase in woody biomass leads to a reduction in grass production and hence a positive feedback will occur where fire is excluded with trees increasing and causing reduced grass growth by limiting light competitive trees (Scholes 2003). As a result the main fuel source for fires is reduced thereby reducing the presence of

fire in the system and favouring further tree recruitment. It is possible that this is a mechanism for the shift of savanna systems towards closed canopy states (Beckage *et al.* 2009). Identifying the threshold at which a savanna shifts from a grass/fire dominated system to a tree/ light competitive system would be a major development for savanna management. A recent study using satellite data and focusing on fire determinants in Africa found that fire spread is severely limited when woody cover exceeds 40% (Archibald *et al.* 2009). Archibald *et al.* (2009) suggest that 40% woody cover represents a threshold, above which fires no longer spread readily. The first aim of this paper is to assess the accuracy of the 40% threshold at a localised scale. In particular it looks at whether there is a threshold tree cover below which grass biomass is suppressed to the extent that the fuel loads are too low for fires to spread. Based on known fuel requirements for grass fires in Africa (Trollope *et al.* 1986) and the findings of Archibald *et al.* (2009) the hypothesis is; grass biomass will be limited to below 200g/m^2 at 40% canopy cover.

One of the obvious and understandable difficulties faced by continental scale analyses with reference to tree cover is that they are unable to define shifts in tree species involved within the relevant study sites. Warman and Moles (2009) state that high rainfall savanna systems support separate stable states, pyrophytic (savanna) vegetation and forests. Brazilian savanna trees have lower leaf area, casting less shade, then forest trees in the same area (Hoffmann et al. 2005). In addition Beckage *et al.* (2009) suggests that certain savanna trees are not only fire tolerant but rather display pyrogenic tendencies that increase the return intervals and intensity of fire within the relevant systems while other species are completely intolerant of frequent fires (Beckage *et al.* 2009). Thus savanna tree species, like grasses, are outcompeted by trees that cast dense shade and therefore may require open, well lit systems to mature. Savanna tree species support fire within the system thereby excluding forest trees and reducing tree on tree competition (*sensu* Bond and Midgley 1995). Certain savanna tree

species aid the spread and frequency of fire by adding litter fuels, especially in North American pine savanna and Australian *Eucalyptus*-dominated savannas (Platt *et al.* 1988; Rebertus *et al.* 1989; Kane *et al.* 2008). The role of litter fuels in African savannas is not well known. It is likely to be negligible where microphyll *Acacias* are the dominant tree but may be important in broad leaved savannas such as miombo. One possible method by which savanna trees could maintain a fuel load that would support fire spread is by reducing the suppression, or even enhancing, understory grass cover (*sensu* Treydte *et al.* 2008). It is suggested that woody forest species maximize their leaf area output to restrict the available light resource and prevent neighboring competitors from spreading into the area occupied by their canopy. This enhances the light competitive ability of forest trees and would result in a deeply shaded understory and the exclusion of light dependant C4 grasses necessary to fuel fires. On the other hand, savanna species are intolerant of shade and have relatively lower leaf area than forest species. Thus savanna trees would cast less shade than forest species and do not limit the grass understory required to carry fires through the system. This paper aims to explore the idea that different tree functional groups (forest and savanna) vary in canopy density and hence light transmittance to the understory. The questions addressed in this study are;

1) At what canopy cover, if any, is grass biomass reduced below the threshold necessary to support fire?
2) Do forest trees cast denser shade than savanna trees?

METHODS

The study was conducted in two different savanna systems within South Africa. The Kruger National Park (S 24.9967; E 31.5919) is in the north east of the country and experiences a summer rainfall pattern with a mean annual precipitation (MAP) around 600mm. Hluhluwe Game Reserve (S28.18483; E32.01653) is in the east of the country and experiences a MAP up to 1000mm.

Site selection

For the purposes of this paper, the term site refers to an area (250m x 250m) within which a number of plots were sampled. The KNP sites were selected based on variations in fire regime and the presence or absence of herbivory. Four different sites were studied to control for the effects of fire and herbivory on grass biomass: no fire and no herbivory, no fire and herbivory, annual fire and herbivory, and fire (five-year burn regime; burnt October 2010) and no herbivory. All sites were within the lowveld bushveld savanna system of the southwest region of Kruger National Park. Site one was the Nkuhlu herbivore exclosure (S 24.98885, E031.77562). The site has kept out herbivores and fire for eight years and represents the control site (no fire, no herbivory). The second and third sites were located in the Skukuza experimental burn plots (EBP's) approximately 15 kilometres southeast of Skukuza (S 25.10021, E031.44991 and S 25.10053, E031.44769). Site two has not been burned in 50 years, and represented a no-fire site with free access to mammal herbivores. Site three was the annual burn string, which represented a recently burned site open to herbivores. Site four was located in the Pretoriuskop herbivore exclosure, which last burned in October 2010 (S 25.12941, E031.23221). The fourth site represented a recently burned area with herbivores excluded. All the KNP sites contained mixed tree communities, dominated by *Terminalia sericea*, *Sclerocarya birrea*, *Combretum apiculatum* and *Acacia nigrescens*.

Site selection in the Hluhluwe-iMfolozi Game Park (HIP) was based on the dominant plant functional type. All sites were in the high rainfall Hluhluwe area of the park. The first site was positioned in dense forest (S 28.05690, E 032.13029) and represented the cut-off or base line for total grass exclusion. The second (S 28.06669, E 032.12061), third (S 28.10442, E 032.04657) and fourth (S 28.06792, E 032.12072) sites were all thicket areas that have been expanding into savanna regions of the reserve and are dominated by *Euclea racemosa* (*schimperi*) and broad leaved species including *Berchemia zeyheri*, *Croton steenkampianus*, and *Sideroxylon inerme*. Finally the fifth (S 28.06235, E 032.05237) and sixth (S 28.06885, E 032.14249) Hluhluwe sites represented savanna systems with the dominant tree species falling within the *Acacia* genus, particularly *Acacia karroo*.

Plots

In this study the term plot refers to a circle with a 5m radius within which all data collection occurred. Within each site, plots were selected along transect lines. Transect lines were 10m apart and their length and number were dependent on the shape and size of the relevant site. Plot selection was randomized by generating random numbers between 5 and 20. These random numbers were taken as meter measurements between each plot along the relevant transect line i.e. the relevant random number designated the distance in meters between the edge of one plot and the edge of the next.

Data collection

Canopy cover was calculated in each plot using a spherical densitometer. Four readings were taken per plot and measured in a different quarter while facing outwards. The recordings were then transformed to % canopy cover using the equation: canopy cover = 100-(#clear blocks * 1.04). Finally all four readings per plot were averaged to get an overall measure. Densiometer readings were compared with light transmittance data at all 60 Kruger National

Park sites. Light transmittance was analyzed using Gap Light Analysis software from photographs taken at ground level using a Canon 180° fisheye lens. Light transmittance should be inversely proportional to canopy cover measurements and therefore a regression should show a close relationship.

Grass biomass was calculated using a calibrated Disc Pasture Meter (Trollope and Potgieter 1986). Within each plot a total of five measurements were recorded, one at the centre of the plot and the other four in their respective quarters. The measurements were then averaged over the whole plot. DPM measurements for KNP were transformed to biomass (gm^{-2}) using the equation: $gm^{-2} = 0.1*(3019+2260*\sqrt{DPM})$ (Trollope and Potgieter 1986). In HIP the DPM was converted using the equation: $gm^{-2} = 12.6 + 26.1*DPM$ (Waldram *et al.* 2008).

Grass species composition was recorded for KNP plots by placing a $1m^2$ quadrat randomly within the plot, and noting grass species and relative abundance. Tree canopy height was measured using a fixed 45% clinometer method (Bruce 1955). Basal area was calculated per plot using a wedge prism (Jorgen and Karsten 1994).

Forest-savanna tree canopy comparison data were collected throughout HIP. Leaf area and stem diameter data were collected regardless of site or plot. Seven sister taxa were selected for comparison (see Table 1). Each group contained at least one forest and one savanna tree species. The data were collected by selecting a single tree from the relevant species. For each tree, data were collected to relate stem diameter to leaf area. Leaf area per stem area was estimated by clipping a selected branch, measuring the stem diameter and weighing the wet mass of all the leaves on the clipping. This was done in increasing increments of stem thickness, from the tip, to the base of the entire tree. The leaf mass of smaller branches removed from larger branches was added to the relevant larger branch leaf weights where necessary. A separate sample of 20 leaves was then collected from the relevant tree. The wet

mass of this sample was recorded before the leaves were pressed and dried. Dry leaves were weighed to create a ratio of wet to dry mass for each species. Finally the dried/pressed leaves were run through a leaf area meter to create a leaf area to dry mass ratio for each species and allowed for the wet leaf mass recordings to be converted into leaf areas.

LAI data was collected by measuring the canopy diameter, used to estimate the radius and calculate the area of the canopy. The total leaf area of each tree was calculated by selecting a branch unit. The leaf area of this branch unit was measured and the number of units within the tree estimated visually by four separate parties. The total leaf area of the tree was calculated using the equation: total tree leaf area = #stem units in entire tree * total leaf area of stem unit. Finally the LAI was calculated using the equation: LAI = total tree leaf area/ area of canopy.

Data analysis

Regression analyses were run comparing canopy cover and average DPM for the 60 KNP and 82 HIP plots to identify at what canopy cover grass biomass was restricted to below $200gm^{-2}$. Akaike's AIC (an information criterion) was run using R for both regressions to select the best model for the data (Aikake 1974).

The probability of fire spread was calculated for 20% categories of canopy cover. This was done for both KNP and HIP by working out the probability of grass biomass exceeding $200gm^{-2}$ for all plots within five ascending canopy cover classes (0-20%, 20-40%, 40-60%, 60-80%, and 80-100%). The same procedure was followed for three other grass biomass thresholds ($150gm^{-2}$, $250gm^{-2}$ and $300gm^{-2}$).

Data of leaf area and stem diameter were log transformed to allow comparison between congeneric pairs using regression analysis. Analyses of covariance (ANCOVA) were run in

STATISTICA to identify differences in leaf area between forest and savanna species with stem diameter as a predictive covariate (Zar 1999).

Congeneric pairs were used to analyze LAI data. T-tests were run comparing savanna species against their relevant forest species.

Table .1. Forest and savanna species arranged in their relevant congeneric pairs.

Congeneric pair name	Forest species	Savanna species
Rhus	*Rhus chirindensis*	*Rhus pentheri*
Dombeya	*Dombeya burgessiae*	*Dombeya rotundifolia*
Harpephyllum	*Harpephyllum caffrum*	*Sclerocarya birrea*
Combretum	*Combretum erythrophyllum*	*Combretum molle*
Acacia 1	*Acacia ataxacantha*	*Acacia Karroo*
Acacia 2	*Acacia robusta*	*Acacia burkei*
Maytenus	*Maytenus heterophylla*	*Maytenus senegalensis*
Euclea	*Euclea natalensis*	*Euclea divinorum*

RESULTS

Regression analysis between light availability and canopy cover revealed a negative relationship, $y = -0.97x + 105.73$ ($r^2 = 0.882$, $P < 0.001$). Canopy cover readings are strongly correlated with the amount of light reaching the grass layer and thus support the use of the densiometer recordings for measuring the shading effect of trees on grass.

The AIC results indicated that a straight line best represented the relationship between tree cover and grass biomass in HIP (wi =0.54), while a third order polynomial was the most

descriptive for the KNP data (wi =0.44). Both regressions indicated negative relationships between canopy cover and grass biomass as expected. The KNP data has the relationship:

$y = -0.003x^3 + 0.445x^2 - 16.60x + 612.6$ (r^2=0.57, p<0.001)

While the HIP data regression equation was:

$y = -5.916x + 619.0$ ($r^2 = 0.50$, p<0.001)

Where y = grass biomass (gm^{-2}) and x = canopy cover (%)

The KNP data indicates a decrease in mean grass biomass from 0% to 20% canopy cover, above which the slope flattens out until 60% (grass biomass= 395.0gm^{-2}) where grass biomass begins to decrease until it is completely restricted over 90% (see Figure 1). The HIP comparison shows that grass biomass is above 200g (382.36gm^{-2}) at 40% canopy cover and is only restricted to below 200g above 70% canopy cover (see Figure 2).

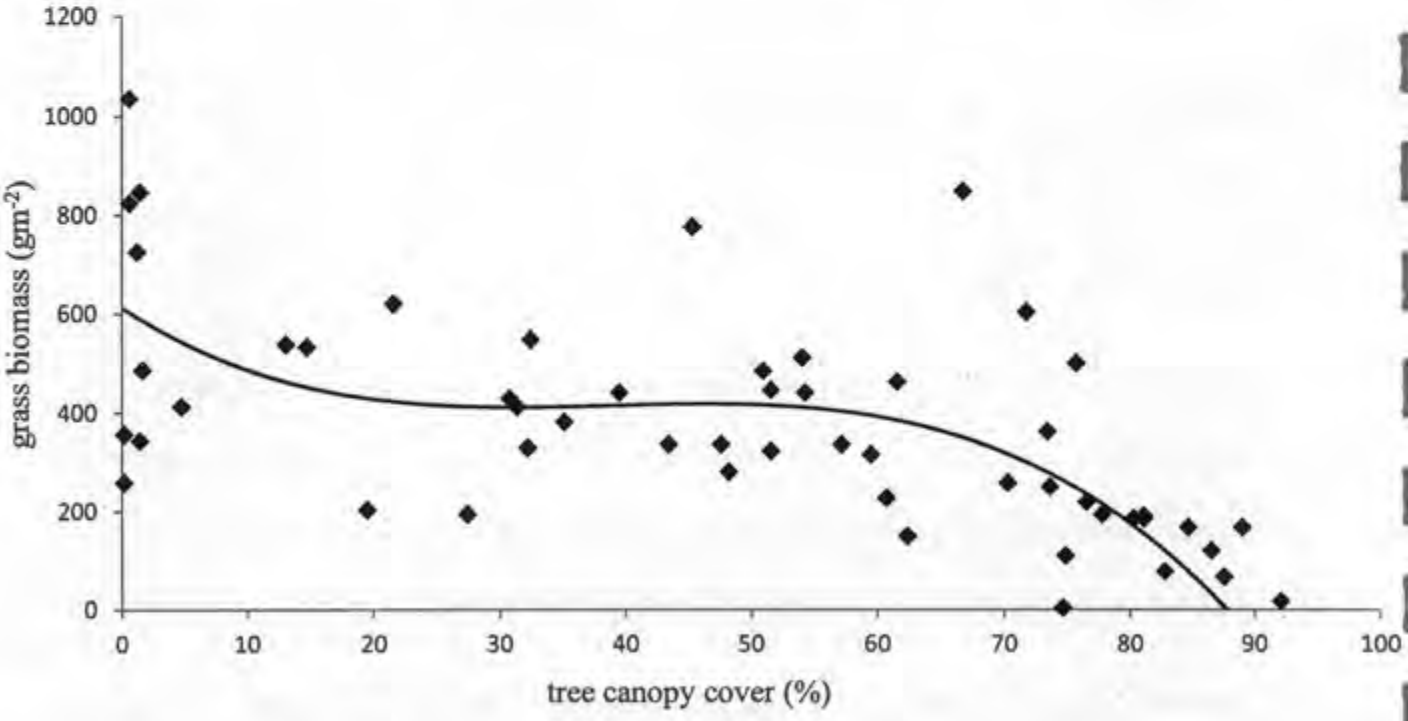

Figure.1. Negative linear relationship between grass biomass and tree canopy cover in the Kruger National Park, $y = -0.003x^3 + 0.445x^2 - 16.60x + 612.6$ (r^2=0.57, p<0.001)

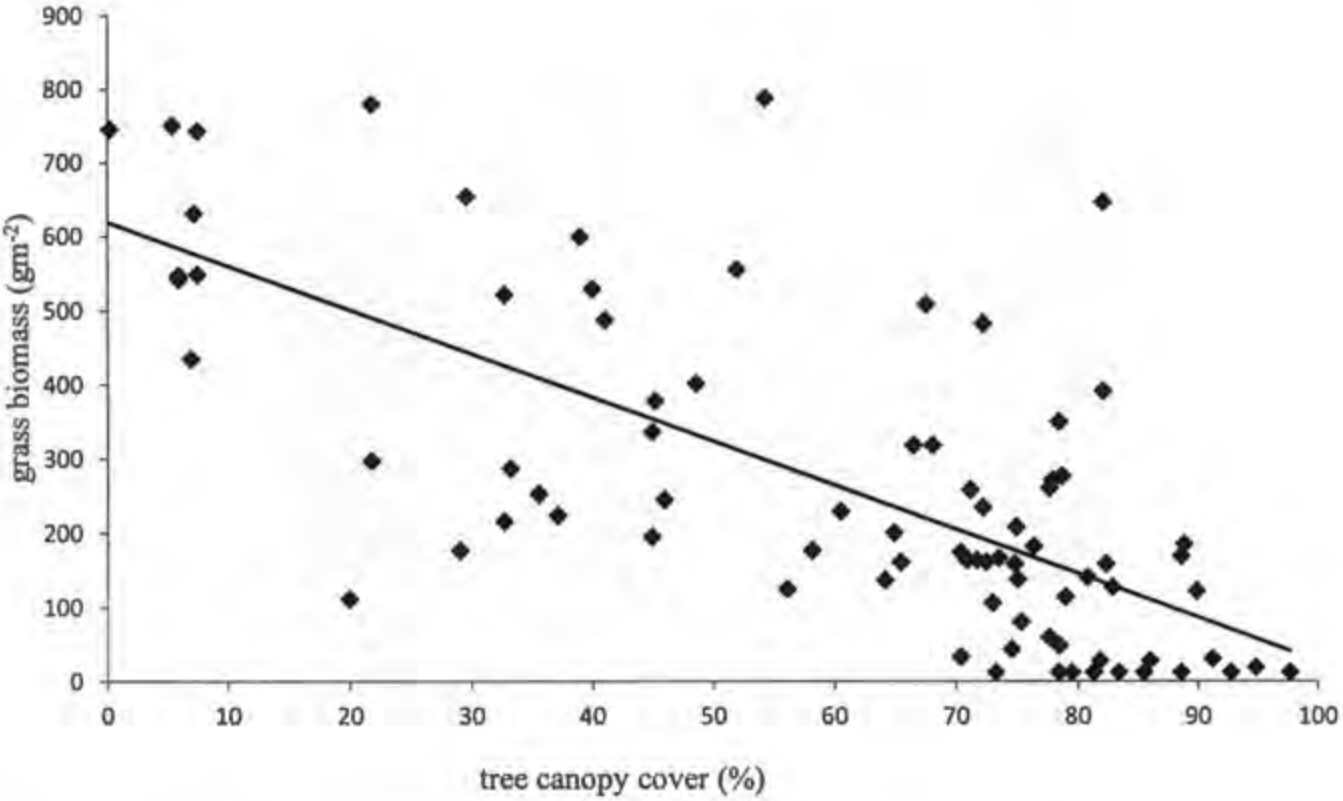

Figure.2. Negative linear relationship between grass biomass and tree canopy cover in the Hluhluwe-iMfolozi Game Park, $y = -5.916x + 619.0$ ($r^2 = 0.50$, $p<0.001$)

Contrary to predictions, there was sufficient grass biomass (Pr>0.70) for fire to spread through the system up to 60% canopy cover in both KNP and HIP (see Figure 3). Between 60% and 80% canopy cover grass biomass in KNP still consistently exceeded 200gm^{-2} (Pr=0.64) and had the potential to carry fire (see Figure 3a). This was not the case in HIP, where at 60%-80% canopy cover only 20% of the plots (Pr=0.24) favoured fire spread (see Figure 4). Against expectations, it was only when canopy cover reached 80% that grass fuel load was too low to support fire spread in all KNP plots (Pr=0) and 89% of the HIP plots (Pr=0.11).

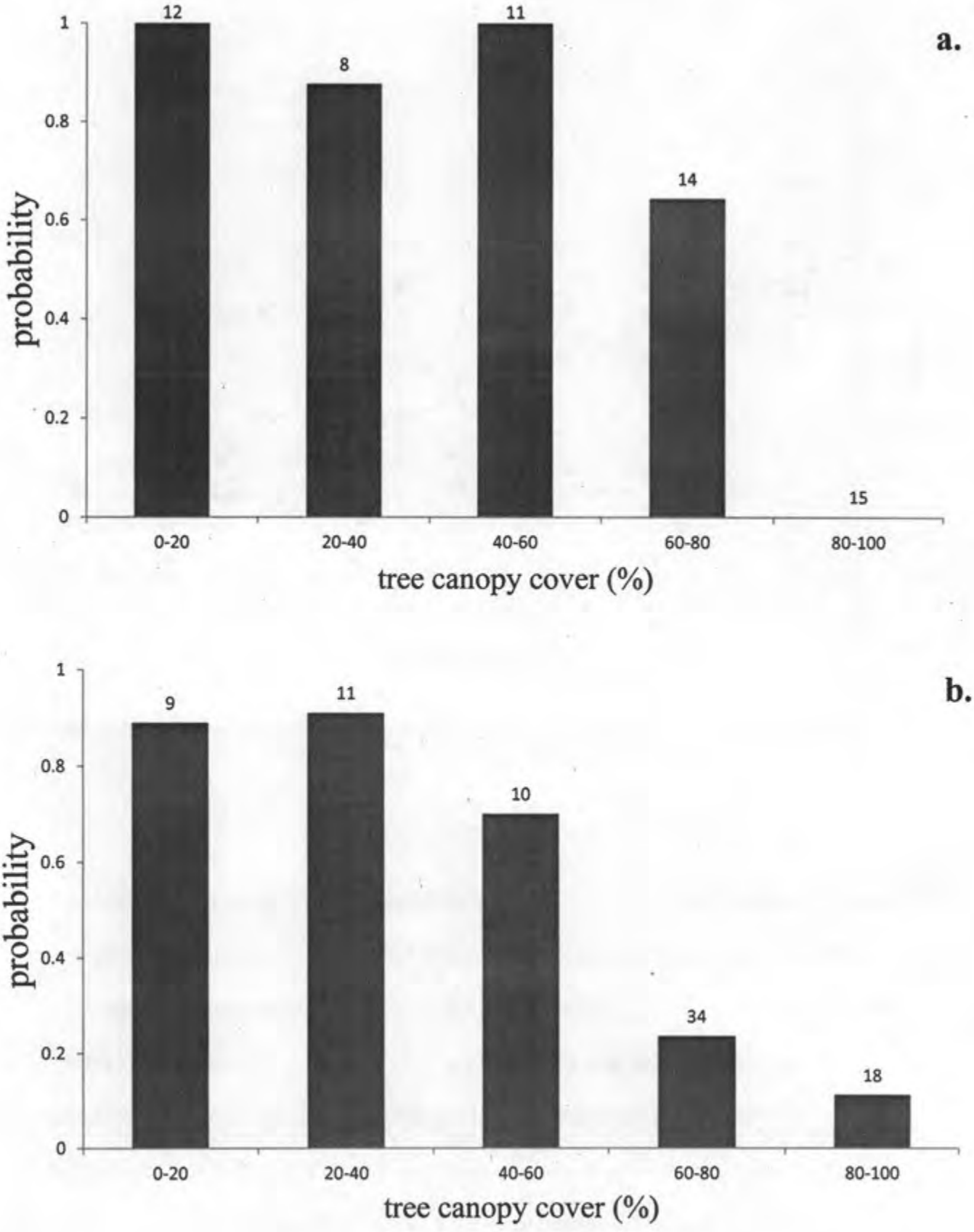

Figure.3. Probability of grass biomass (gm^{-2}) in Kruger National Park (a) and in Hluhluwe-iMfolozi Game Park (b) exceeding $200gm^{-2}$ for five different intervals of canopy cover (numbers above bars represent number of plots in each canopy cover interval)

Figures 4 indicates that very little variation was observed in the probability of grass fuelled fire spread when the threshold grass biomass was altered. At an estimated 300gm^{-2} of grass biomass required for fire spread, 60% of HIP plots and 100% of KNP plots contained sufficient grass fuel to support fire spread between 40% and 60% canopy cover. Grass biomass at 80%-100% canopy cover was sufficient to support fire spread in over 25% of both HIP and KNP plots when a minimum thresholds of 150gm^{-2} for fire spread was used.

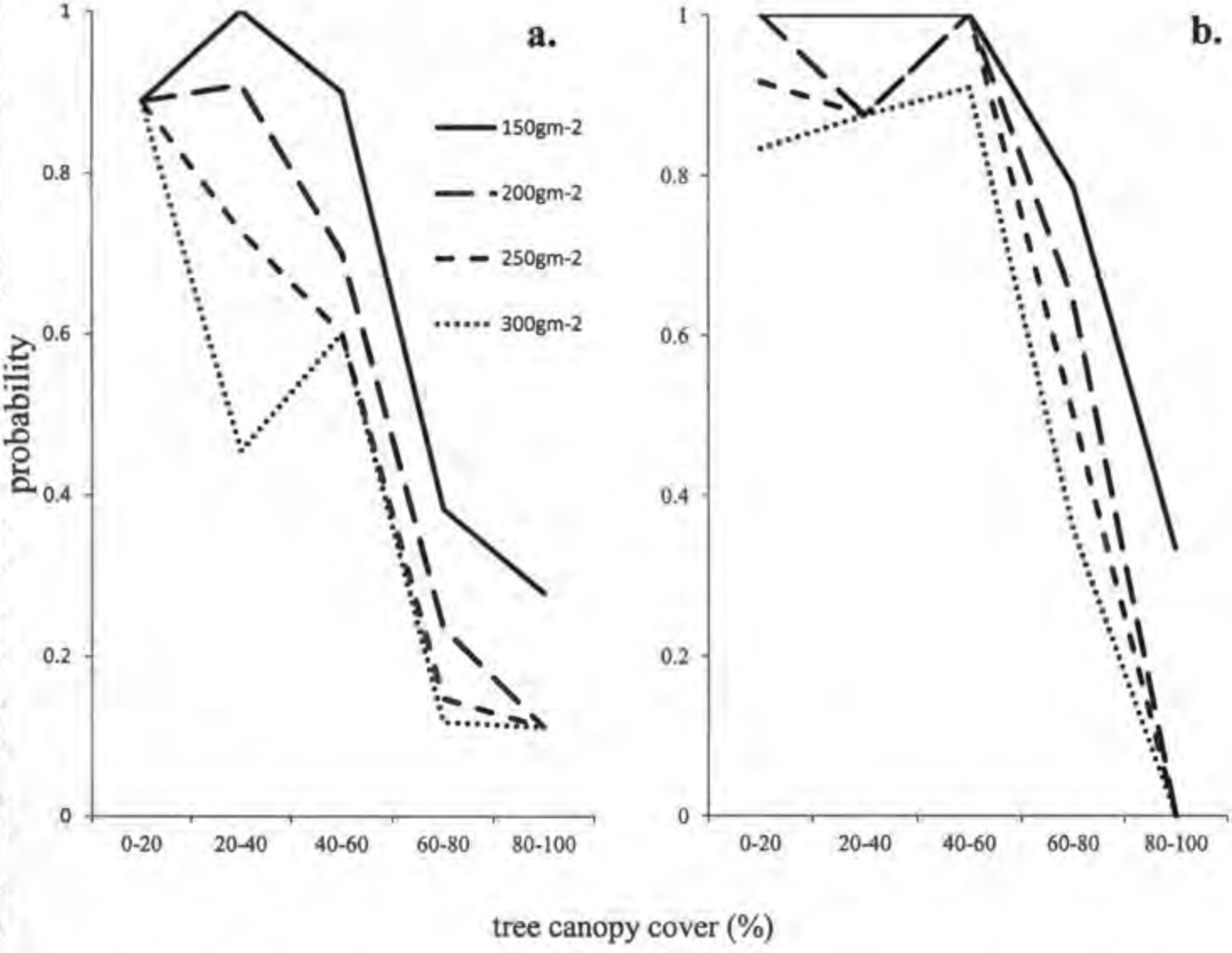

Figure.4. Probability of grass biomass (gm^{-2}) in Kruger National Park (a) and in Hluhluwe-iMfolozi Game Park (b) exceeding four different minimum thresholds of grass fuel for fire spread in relation to canopy cover.

Leaf area increased with increasing stem diameter in all species (see Figure 5). The congeneric pairs of *Rhus* and *Dombeya* showed no significant difference between forest and savanna leaf area for a given stem diameter (see Table 2). The congeneric pairs of *Harpephyllum*, *Combretum*, *Acacia* 1 and *Acacia* 2 indicated forest species having significantly higher leaf area than savanna species for a given stem diameter. The *Maytenus* and *Euclea* pairs showed the opposite relationship with savanna species having greater leaf area for any given stem diameter than forest species.

Table .2. Summary of ANCOVA results for all congeneric pairs (see Table 1 for species names) comparing forest and savanna leaf areas with stem diameter as a predictive covariate ($p<0.001$**, $p<0.05$*)

Congeneric pairing	Stem diameter MS	p-value	Species MS	p-value
Rhus	5.238	**	0.073	0.163
Dombeya	3.874	**	0.011	0.095
Harpephyllum	6.532	**	0.413	**
Combretum	7.382	**	0.057	*
Acacia 1	8.955	**	0.785	**
Acacia 2	7.142	**	0.207	*
Maytenus	3.2	**	1.753	**
Euclea	8.79	**	0.28	**

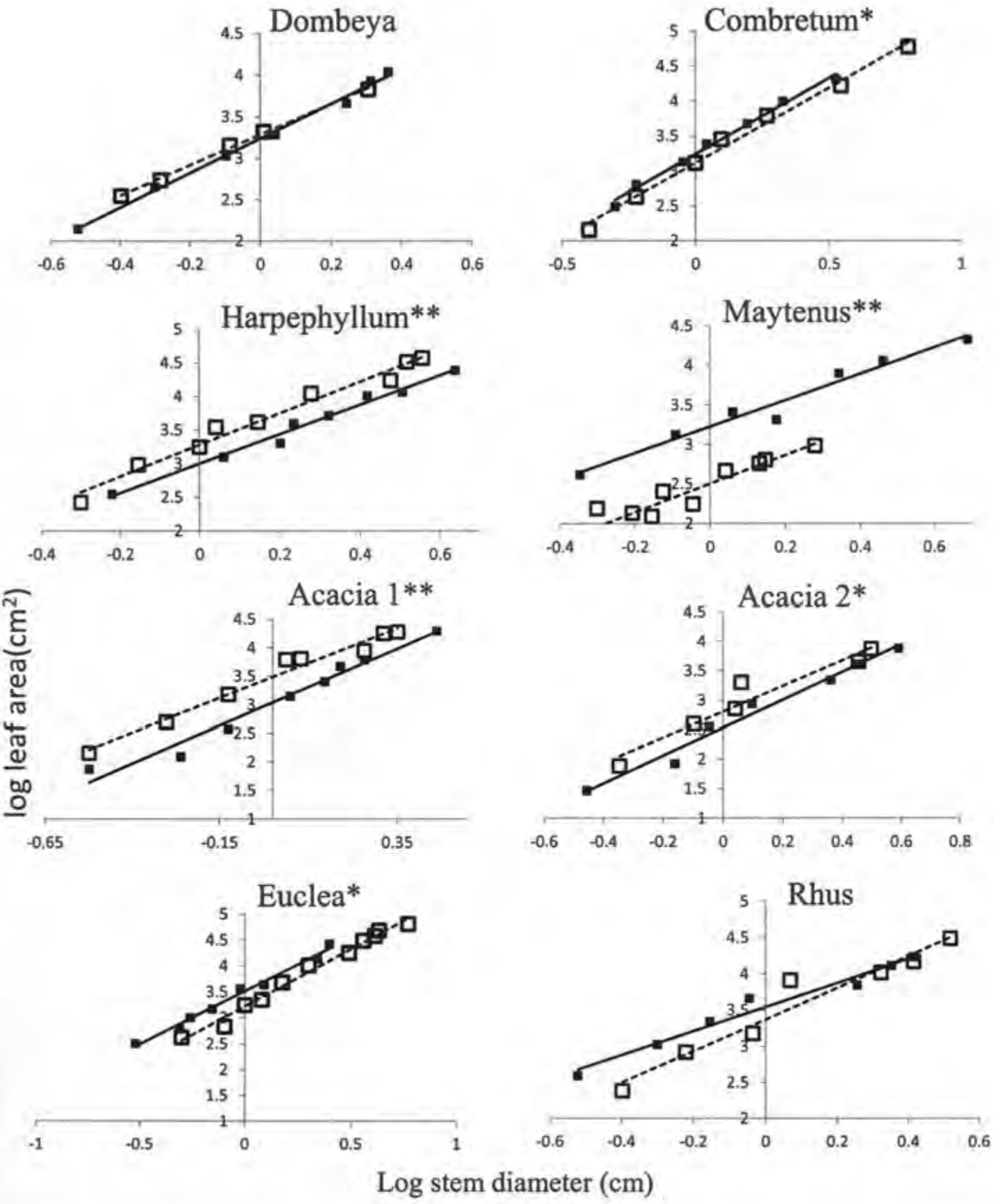

Figure.5. Relationship between leaf area and stem diameter of congeneric savanna and forest species. Both axes log transformed. See table 1 for species names. Open squares and dotted lines represent forest species while closed squares and solid lines represent savanna species ($p<0.05$*, $p<0.01$**)

Figure 6 shows that LAI was higher in forest species than savanna species for four congeneric pairs but only significantly different in *Rhus* ($t=9.15$, $p<0.01$) and *Combretum* ($t=2.38$, $p<0.05$). The *Maytenus* pairing and both *Acacia* groupings showed higher LAI in savanna species than forest; however the only significant result was that of *Maytenus* ($t=3.93$, $p<0.01$).

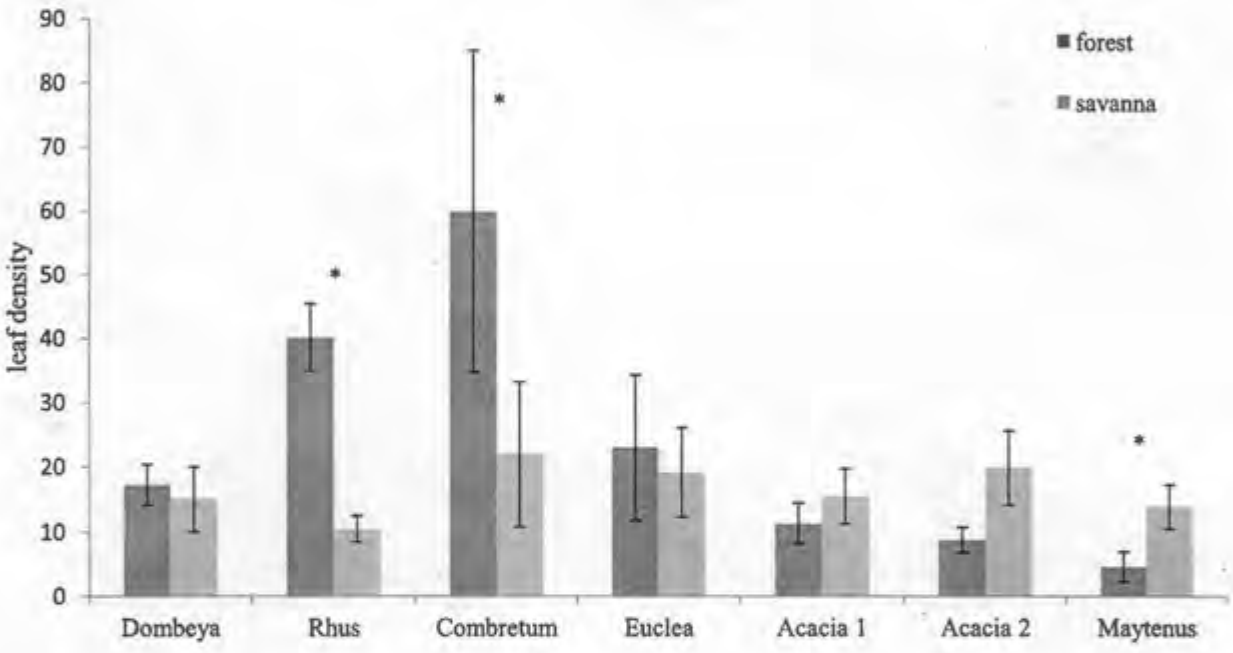

Figure.6. Comparison of forest and savanna LAI values (error bars represent standard error, $p<0.05$*, $n=3$)

DISCUSSION

The grass biomass at different canopy covers in both KNP and HIP indicated that fuel load would not support fire spread above 80% canopy cover (see Figure 1, 2 and 3). Archibald *et al.* (2009) suggested fire was limited at 40% canopy cover. However, it is clear from the data collected here that one can expect sufficient fuel for fire at 40% canopy cover in both KNP and HIP (see Figure 1, 2 and 3). At a fuel estimate known to carry fires intense enough to burn woody vegetation (300gm^{-2}), grass biomass is still sufficient to support fire at a canopy

But this is an extrapolation based on grass biomass & not fire probability

cover of over 50% in both KNP and HIP (see Figure 1 and 2). From this study, it is not possible to say that 40% canopy cover does not result in fire exclusion, but the data certainly indicate such a relationship is not related to grass fuel loads. Although there is the possibility that another unforeseen relationship accounts for fire exclusion observed in continental scale data, it is important to highlight a more fundamental issue: the difficulty in relating satellite recorded tree cover to that of ground level measurements. In this particular case the MODIS Vegetation Continuous Fields 500m data set utilised for continental analysis was measured by sensing equipment that only records canopies above 5m in height (Hansen *et al.* 2003). Although this is high quality satellite data it still fails to pick up the extant canopy cover evident to the grass layer. If a simple understanding of recruitment is to be applied it should become clear that if 40% of the tree cover is above 5m in height there should be equal if not more trees present at lower heights (Menaut *et al.* 1990). It is probable that when satellite data ~~is~~ are indicating 40% canopy cover the actual woody cover is higher. It is thus necessary to develop an understanding of what satellites are measuring at the ground level if satellite data is to be used for vegetation analyses.

Data from KNP and HIP showed clear differences in fire spread probability at the intermediate canopy cover of 60% to 80%. HIP showed a lower probability of supporting a fire at this canopy cover bracket than KNP. Under the same light conditions, grasses in one area are persisting in high enough quantities to support fire while being in insufficient quantities in another. Scholes (2003) suggested three main restrictions of grass growth with reference to an increase in woody biomass/canopy cover 1) nutrient limitation 2) water availability and 3) shade intolerance. In light of this, the fact that the higher MAP and nutrient soils of HIP have lower probabilities of supporting sufficient fuel than the drier nutrient poor KNP is surprising. One possibility is that the different vegetation types at the two different regions are playing a role i.e. HIP has dense thicket that accounts for the

I don't understand?

majority of the intermediate canopy cover in the region, while KNP lacks a similar vegetation structure and thicker canopies are more likely the result of single large trees. Extrapolating from this idea, it is possible that in KNP single large trees are promoting understory growth to a certain extent (*sensu* Treydte *et al.* 2008) whereas in the HIP, groupings of trees in thickets generate a more intense competition for below ground resources limiting grass growth (Scholes 2003). Investigations into patch dynamics indicate similar results in encroaching shrub species (Meyer *et al.* 2007b). Meyer at al. (2007b) argued that as shrub size and density increased, below ground overlap of roots increased and resulted in greater response to water and nutrient limitation. Similarly in thicket regions of HIP where the number of stems are higher than that of KNP the result may be increased below ground competition and resultant exclusion of less competitive grasses. The different patterns in the two parks highlight the need for a more local understanding of differences in vegetative structure, particularly if management plans are to be developed.

Forest vs. savanna trees

The congeneric pairs failed to show a consistent pattern of higher leaf area for a given stem diameter in forest than savanna species, contrary to predictions. *Maytenus heterophylla* was the only forest species that had significantly lower leaf area per stem than its savanna pairing (see Figure 5). This may be the result of energy expended by both species in protection against browsing. This could limit the amount of leafy output possible even in forest species, but fails to explain the higher leaf area in the savanna species. Another possibility is that, as a small, shrubby genus the forest species does not make up the main canopy of forests and an understory shrub is largely uninvolved in light competition, utilising a different strategy.

Combretum erythrophyllum, *Acacia ataxacantha*, *Acacia robusta* and *Harpephyllum caffrum* all had significantly greater leaf area than their respective savanna species (Figure 5). Tree

species are known to have a fixed relationship between leaf area and stem diameter (Waring *et al.* 1980; Waring 1983, Vertessy *et al.* 1995). Light is known to be a limiting resource in forest systems (Waring 1983). As a result increased photosynthetic area in the form of higher leaf area per stem will give trees a competitive advantage, not only in accessing light but also in shading possible competition. For these congeneric pairs it appears that forest trees create denser canopies with more light interception than savanna trees and hence reduce light below their canopies. This gives strength to the idea that forest species are producing more leaf area than is required to produce wood. Greater shade cast by forest trees would reduce understory growth with the indirect advantage of limiting fire in the local area. On the other hand, pyrophytic savanna species cannot create dense shade and the microhabitats created by savanna trees may well enhance grass biomass (*sensu* Treydte *et al.* 2008), allowing fires which indirectly reduce tree on tree competition.

The overall forest vs. savanna comparison of leaf area per stem diameter failed to show significant differences and thus did not support the overall hypothesis. However, there is enough support from specific congeneric pairs to warrant further investigation. A controlled experiment looking at the light environment under single trees from savanna and forest congeneric pairs should provide more defendable outcomes when comparing the two vegetation types. If the number of species compared was increased this could allow for a more general idea of the differences in light conditions under savanna vs. forest trees. Ultimately this would make it possible to assess whether any difference between the two canopy types is significant enough to change their effect on the understory grass layer.

There was no consistent difference between LAI of forest and savanna species, contrary to predictions. *Maytenus heterophylla* and both *Acacia* forest species had lower LAI than their savanna pairings (Figure 6). This is not surprising for *Acacia ataxacantha*, which grows as a climber creating a broken up canopy that is unlikely to be dense due to the lack of supportive

material (Palgrave 1983). Even so, neither Acacia groups showed significant differences (see Figure 6). *Maytenus heterophylla* showed a significant difference and again this may be due to issues discussed earlier. The other four congeneric pairs all followed the predicted relationship with forest species having a higher LAI than related savanna trees.

Combretum erythrophyllum, *Rhus chirindensis*, *Dombeya burgessiae* and *Euclea natalensis* all had higher LAI values than their respective savanna species, although only the former two were significant. This fits the pattern reported by Hoffmann *et al.* (2005) for Brazilian forest-savanna. It certainly appears that forest species are creating more complete canopies and again it would be worth testing the different effects this may have on understory canopy through both light limitation and reduction in soil moisture (*sensu* Treydte *et al.* 2008).

Conclusion

Neither the KNP system nor the HIP system supported the hypothesis that fire spread is limited above 40% canopy cover. Instead the data suggested that fuel at the levels necessary to carry fire were only consistently restricted above 80% canopy cover. It is clear that there are substantial discrepancies between the predicted and observed values. Remotely sensed tree cover needs to be more accurately correlated with ground level measurements to evaluate local values for the threshold tree cover at which grass fuel loads no longer support fire spread.

Finally the investigation into the dynamics surrounding forest and savanna tree canopy structure lent some support to the idea that forest species have denser canopies than their savanna counterparts. It is logical that an increased photosynthetic area will lead to increased interception of light and this will no doubt increase the severity of light limitation at the ground level. It is tentatively suggested that savanna species produce the required amount of leaf area to maintain growth, while forest species saturate their canopies to shade out

competitive neighbours. The indirect effect of this is that savanna species support understory grass growth while forest species suppress grass. Whether or not the difference is large enough to drive changes in fire regime has still to be investigated.

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